Identification of quantitative trait loci affecting carcass composition in swine: I. Fat deposition traits

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J Anim Sci 1998. 76:2247-2254.

Identification of Quantitative Trait Loci Affecting Carcass Composition in Swine: I. Fat Deposition Traits

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ABSTRACT: One of the major determining factors in the price of market hogs today is backfat depth. Therefore, identification of regions of the genome affecting this trait could be very useful to the swine industry. A large resource population (n = 540) was developed by backcrossing F_1 Meishan-White composite females to either Meishan or White composite boars. A genomic scan was conducted by genotyping all animals with microsatellite markers spaced at ~20-cM intervals across the entire porcine genome. Breed of origin for all chromosomal segments was determined using multipoint linkage procedures, and a least squares regression analysis was conducted. Nominal *P*-values were converted to a genome-wide level of significance to adjust for the numerous tests conducted. Traits analyzed were backfat depths at the first rib (FRIB); 10th rib (10th); last rib (LRIB); last lumbar (LLUM) vertebra; the average of FRIB, LRIB, and LLUM (AVBF); and weight of leaf fat (LEAF). Significant quantitative trait loci (QTL) were detected on chromosomes 1, 7, and X. Suggestive evidence for QTL was present on chromosomes 5, 8, 9, 10, 13, and 14. Genotypic means for the loci detected indicated a predominantly additive mode of inheritance. Meishan alleles produced fatter pigs for all loci except those on chromosomes 7 and 10. Additional research should be conducted to refine the estimated position of each QTL and its effect and determine epistatic interactions. These loci should be evaluated in other germplasms to determine whether allelic variation at the QTL exists in other breeds.

Key Words: Pigs, Quantitative Traits, Fat, Genomes, Mapping

 J. Anim. Sci. 1998. 76:2247–2254

Introduction

Now that a comprehensive map has been developed for the porcine genome (Rohrer et al., 1996), genomic scans to detect quantitative trait loci (**QTL**) can begin. In swine, three publications have reported identification of QTL using genomic scans (Andersson et al., 1994; Casas-Carillo et al., 1997; Rathje et al., 1997). Only one study included body composition traits, and the researchers identified QTL affecting growth, fat deposition, and length of small intestine in a F_2 population of Large White and European wild boar (Andersson et al., 1994). The QTL associated with average backfat and abdominal fat percentage was located on chromosome 4 (SSC 4p), and this has been verified in subsequent generations of the population (Marklund et al., 1996). The other two studies used crosses between lines developed in long-term selection studies for either reproduction (Rathje et al., 1997) or growth traits (Casas-Carillo et al., 1997). To date, there are no reports from populations using crosses between Chinese and western-breed germplasm in a genome-wide scan.

The swine mapping program at the U.S. Meat Animal Research Center (MARC) is attempting to map loci that affect production efficiency in swine. The objectives of this research were to map QTL that control backfat because of its economic importance and relatively high heritability. We report the detection of QTL for fat accretion identified with a genome-wide scan including 156 markers spaced at intervals of ~20 cM in a reciprocal backcross population of Meishan and White composite with 540 progeny.

Materials and Methods

Population

A three-generation resource population was developed by first mating Meishan males and females to White composite females and males, respectively. Five animals within each breed by sex subclass were selected. All F_1 (n = 41) females were mated to either the Meishan or White composite boars that had been used to produce the F_1 animals. Producing inbred litters was generally avoided. The F_1 females had the

Received February 5, 1998.
Accepted May 15, 1998.

Table 1. Phenotypic means for dependent variables and covariates

Trait	¾ Meishan-¼ White composite	¼ Meishan-¾ White composite
Hot carcass weight, kg	57.5	63.3
First-rib backfat, cm	4.3	3.7
Tenth-rib backfat, cm	3.3	2.6
Last-rib backfat, cm	2.3	2.1
Last-lumbar backfat, cm	2.9	2.4
Leaf fat weight, kg	1.2	1.1

opportunity to produce two litters with some females bred back to the same boar, and others were intentionally mated to a different breed of boar. The resultant progeny were either ¾ Meishan-¼ White composite or ¼ Meishan-¾ White composite.

Males included in this study were castrated. Most of the male pigs and approximately half of the female pigs (randomly selected) were slaughtered when they weighed approximately 100 kg. Carcasses were skinned, rather than scalded and dehaired, so error variances for measures of fat thickness were larger than normal. Hot carcass weights were recorded, and the carcasses were chilled overnight. Carcasses were processed 24 h after death. Depth of backfat over the midline was recorded at the first rib (**FRIB**), last rib (**LRIB**), and last lumbar vertebra (**LLUM**). Carcasses were ribbed between the 10th and 11th ribs, and fat depth was measured perpendicular to the skin, three-fourths the distance from the medial side of the longissimus muscle (10th-rib fat thickness; **10th**). Leaf fat was removed from the carcass and weighed (**LEAF**). Phenotypic means for animals of each breed-type are presented in Table 1.

Genetic Markers

Markers were selected from the map produced by Rohrer et al. (1996; http://sol.marc.usda.gov/) based on their position, ease of scoring, number of alleles, and ability to be amplified in a multiplex PCR reaction. Maximum interval desired was 20 cM; however, some regions were greater than 20 cM because of a lack of useful markers. Markers and their PCR groups used were as reported (Rohrer et al., 1997). Selected markers spanned the linkage map, and F_1 females possessed heterozygous genotypes for 91% of the markers (on average).

Statistical Analyses

The QTL were detected using a least squares procedure similar to that described by Haley et al. (1994). Genotypic data were imported into CRI-MAP 2.4 (Green et al., 1990), marker order was as specified by Rohrer et al. (1996), and the CHROMPIC option was implemented. The software was often unable to run the entire linkage group in a single analysis, so overlapping analyses were conducted for the affected chromosomes. First, the beginning of the linkage group was analyzed by eliminating the last marker of a group until the software could run the analysis. Then, the latter portion of the linkage group was analyzed by removing markers in the beginning of the group. Usually only one or two markers needed to be eliminated, and all chromosomes had at least three markers in the overlapping region.

Transmission of alleles from parent to offspring was based on the CHROMPIC output. Grandparental breed of origin at a given region was determined as a probability of inheriting a Meishan segment from the F_1 mother by tracing back the flanking informative markers to the grandparental chromosomes. Probability of receiving a Meishan allele in each generation was based on the flanking marker information and the equation presented in Haley et al. (1994). Relative position of each marker was based on sex-averaged maps for the autosomal chromosomes and the female map for X reported by Rohrer et al. (1996). These probabilities were then used as regression coefficients to determine the likelihood that a QTL that affects the dependent variable exists at that location of the genome.

Linear contrasts were designed to estimate a and d, as described by Falconer (1981), where a is the value for animals homozygous for alleles derived from Meishan, $-a$ is the value for animals homozygous for alleles derived from White composite, and d is the value for animals heterozygous. Thus, the difference in expected performance for the alternate homozygous genotypes equals $2a$. The contrast for a compared the difference in phenotype of animals inheriting a Meishan vs a White composite allele from the F_1 dam across the ¾ Meishan-¼ White composite and ¼ Meishan-¾ White composite pigs. The contrast for d assumed an equal genotypic value for heterozygous individuals despite the origin of the Meishan allele (no imprinting).

Analyses for QTL on chromosome X were conducted with two methods. One test fit a single degree of freedom contrast estimating a, and the other estimating a within males and females separately and d within females (3 df). Significance tests were similar for both analyses. Estimates of a in males and females were similar in the second model, and all estimates of d were virtually null; therefore, the single degree of freedom model, estimating a across sexes, will be reported.

Initial scans were conducted by estimating the probability of a QTL every 1 cM along the chromosome and extending the linkage group by 10 cM in each direction. Occasionally, probabilities were determined from only a single marker because the region was not flanked by informative markers. Most of these instances were limited to regions outside of the linkage group.

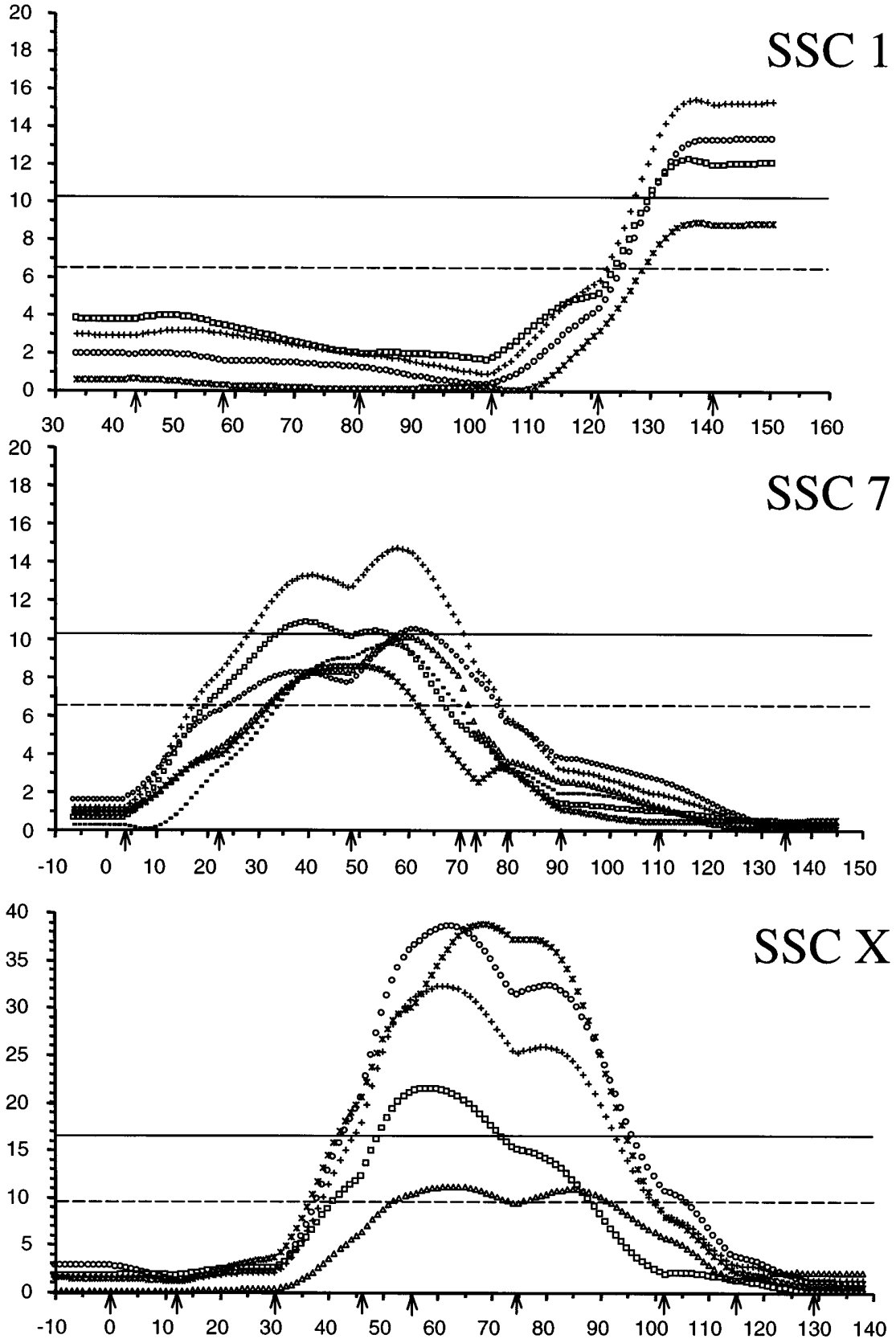
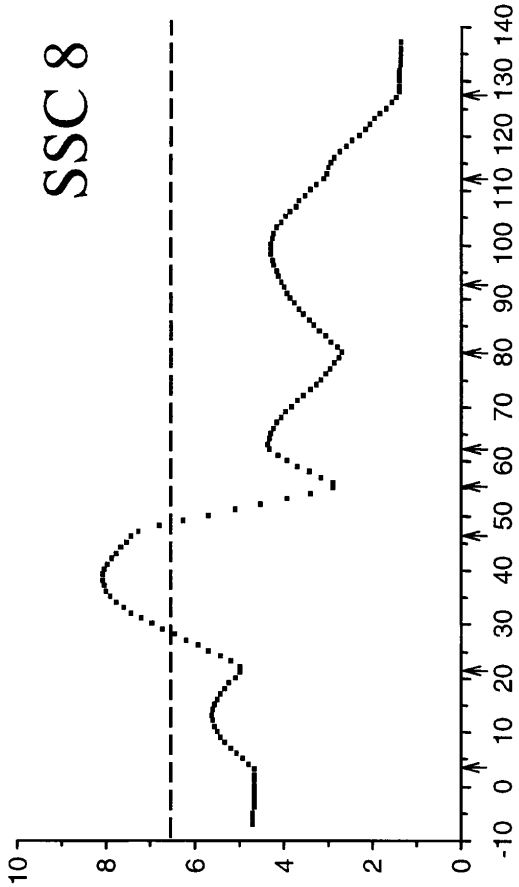
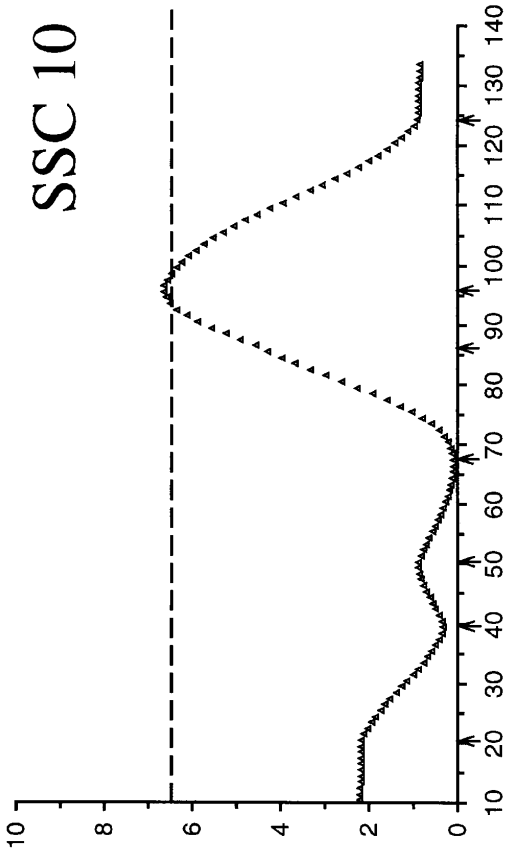
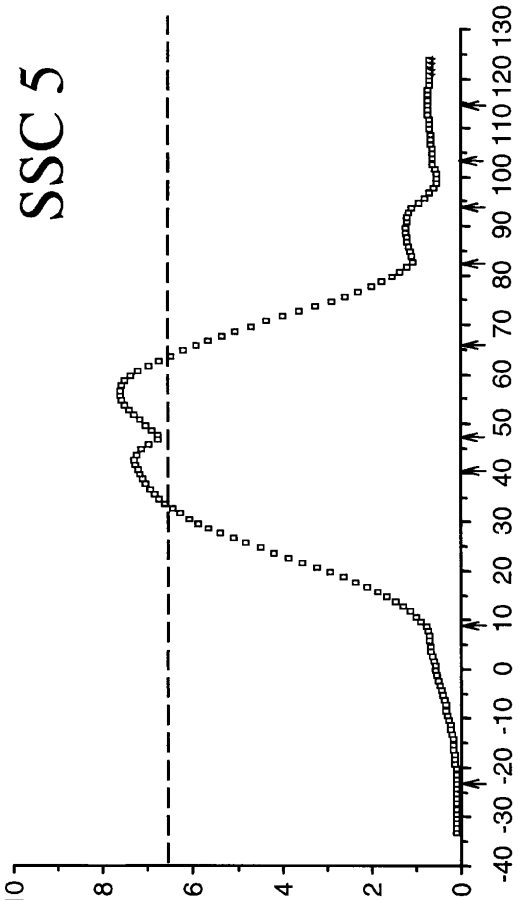


Figure 1. F-ratio curves for analyses with at least one significant association to a trait. Numerator degrees of freedom were two for chromosomes 1 and 7 and only one for the X chromosome. The x-axis indicates the relative position in the linkage map based on Rohrer et al. (1996). The y-axis represents the F-ratio. Arrows on the x-axis indicate a marker position. Horizontal lines indicate threshold values for significant (solid line) and suggestive (dashed line) genome-wide significance. △ = first rib, o = last rib, □ = last lumbar, * = tenth rib, + = average backfat, ■ = leaf fat.







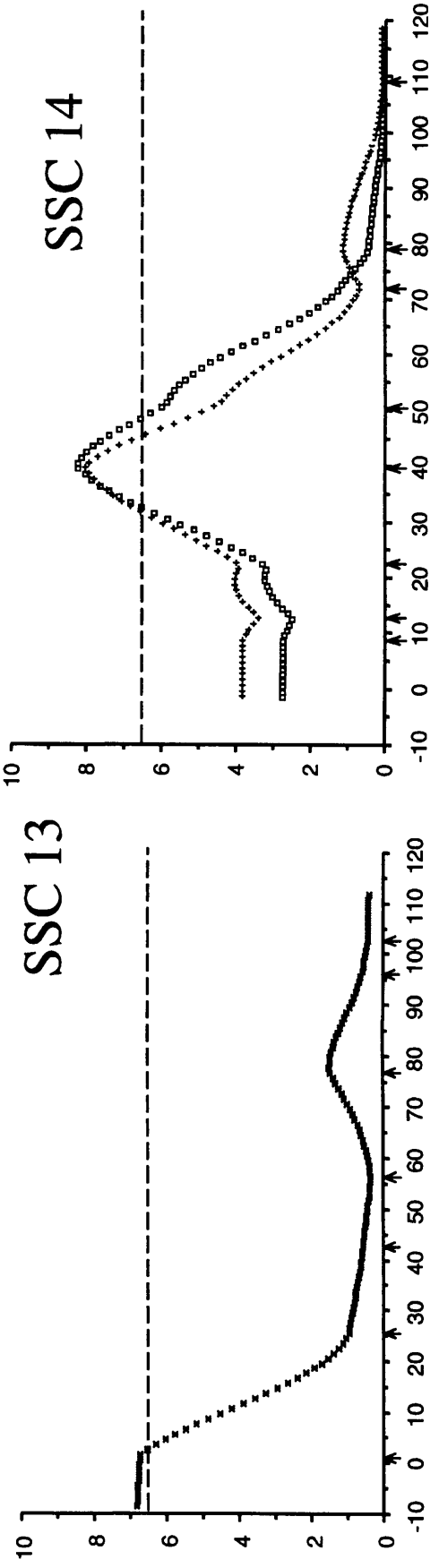


Figure 2. F-ratio curves for associations with suggestive evidence of linkage to a QTL. The x-axis indicates the relative position in the linkage map based on Rohrer et al. (1996). The y-axis represents the F-ratio. Arrows on the x-axis indicate the position where a marker was present. Chromosome 5 was extended with marker SW413, which mapped 23 cM above SW491, thus its position at –23 on the diagram The dashed horizontal line indicates the threshold value for suggestive genome-wide significance. △ = first rib, ○ = last rib, □ = last lumbar, *tenth rib, + = average backfat, ■ = leaf fat.

All statistical models were similar. Fixed effects were fitted for the mean, sex, season of birth, and breed composition (¾ Meishan-¼ White composite vs ¼ Meishan-¾ White composite) with a covariate for hot carcass weight included to adjust all carcasses to a common weight.

It was assumed that QTL alleles were fixed for different alleles within each progenitor line. Even though this assumption is surely incorrect, the algorithm is still effective if the mean allelic effect from the Meishan maternal grandparent is different from the mean White composite maternal grandparental alleles. This assumption does not increase the number of false-positives (type I error); rather, it decreases the power to detect all QTL segregating in the resource population. Therefore, the estimates of *a* and *d* are actually estimates of mean allelic effects between the two grandparental breeds.

Nominal significance values were determined from the F-ratio curve using the appropriate degrees of freedom (numerator df = 2 for autosomal regions and 1 for SSC X; denominator df ranged from 530 to 532). Expected number of false-positives per genome-wide scan was determined based on the equation presented in Lander and Kruglyak (1995), where genome-wide significance = $(C + 2 \cdot G \cdot \rho \cdot f \cdot dfn) \times (1 - probf(f, dfn, dfd))$; f is the F-ratio, dfn is the numerator degrees of freedom, and dfd is the denominator degrees of freedom. Values for the swine genome used were C = 19 (19 chromosomes), G = 25 (25-morgan genome length), and ρ = 1.0. For autosomal tests, critical values for suggestive and significant linkages were approximately 6.6 and 10.15, respectively. Thresholds for 95% confidence intervals for each QTL peak were determined based on the noncentrality parameter.

Results

The F-ratio curves are plotted in Figures 1 and 2 for all regions with a suggestive level of significance or greater. Table 2 presents the location of the maximum F-ratio, estimates for *a* and *d*, and the number of false-positives expected per genome-wide scan for each region graphed. Three genomic regions were highly significant for measures of subcutaneous fat deposition over the back. These regions were on chromosomes 1, 7, and X and generally had at least a suggestive level of significance for all five measures of backfat. The Meishan alleles for the QTL on chromosome 1 and X conferred greater fat depth, as would be expected based on differences between the grandparental breeds (Young, 1992) and trends observed in the backcross animals (Table 1). However, individuals homozygous for Meishan alleles at the putative QTL on SSC 7 were leaner than those homozygous for White composite alleles. These results are typical of the phenomenon defined as transgressive variation

Table 2. Putative QTL detected with at least a suggestive level of significance

Trait and chromosome	Position, cM[a]	Genotypic value[b]		Significance		
		a	*d*	F-ratio	nominal[c]	genome[d]
First-rib backfat						
7	60 (24–77)	–.307	.042	10.1131	.000049	.05039
10	95 (78–117)	–.193	.038	6.652	.001402	.95893
X	63 (39–110)	.250	NA[e]	11.2134	.000870	.50409
Tenth-rib backfat						
1	138 (124–150)	.292	–.010	8.9301	.000153	.13976
7	51 (18–70)	–.198	.043	8.5787	.000215	.18883
13	–8 (–8–16)	.099	.092	6.8153	.001195	.83726
X	68 (47–92)	.419	NA	38.8401	.000000	.00000
Last-rib backfat						
1	150 (126–150)	.340	–.001	13.3642	.000002	.00295
7	62 (16–86)	–.288	–.007	10.4219	.000036	.03855
X	63 (47–93)	.335	NA	38.5097	.000000	.00000
Last-lumbar backfat						
1	136 (124–150)	.339	–.007	12.245	.000006	.00786
5	57 (21–74)	.275	.045	7.5905	.000562	.43717
7	40 (17–73)	–.277	.035	10.8007	.000025	.02774
14	41 (24–63)	.258	–.001	8.1849	.000316	.26419
X	59 (41–89)	.295	NA	21.4398	.000005	.00501
Average backfat						
1	138 (126–150)	.298	–.003	15.4415	.000000	.00047
7	58 (20–76)	–.286	.024	14.7204	.000001	.00089
14	40 (–1–58)	.187	–.014	8.0498	.000360	.29634
X	61 (45–93)	.292	NA	32.331	.000000	.00004
Leaf fat weight						
7	56 (28–76)	–.110	.015	9.6383	.000077	.07597
8	38 (–7–74)	.118	–.007	8.0347	.000365	.30016
9	34 (17–62)	.109	–.003	7.7342	.000489	.38720

[a]Relative position is in centimorgans, based on maps developed in Rohrer et al. (1996), and values in parentheses represent the 95% confidence interval.
[b]Genotypic values are as described by Falconer (1981) in units of centimeters for backfat and kilograms for leaf fat weight.
[c]Probability of a false-positive for a single hypothesis test.
[d]Expected number of false-positives per genome-wide scan based on equations from Lander and Kruglyak (1995).
[e]NA = not .

(i.e., when the estimated allelic effects for a QTL are opposite of expectations based on breed means).

Five additional chromosomal regions were detected with an expected false-positive rate of one per genome scan. A 95% confidence interval for number of false-positives in these five regions is between zero and three (based on a binomial distribution); therefore, at least two associations are expected to be real QTL. The QTL on SSC 8 and 9 displayed suggestive linkage for leaf fat and four regions presented evidence of QTL for backfat on chromosomes 5, 10, 13, and 14. The consistent finding for the region on SSC 14 for LLUM and AVBF would tend to indicate that this QTL may be real.

Ten additional associations had F-ratios greater than 5.0 and merit mentioning. Two regions approached suggestive linkage for LEAF on SSC 12 and 15 at positions 0 and 19 cM, respectively. Quantitative trait loci for FRIB may exist on chromosomes 1, 8, 14, and 17 at positions 136, 69, 40, and 63 cM, respectively. The analysis of SSC 2 for 10th and LRIB produced broad curves with values exceeding 5.0. The analysis of LLUM detected a peak on SSC 15, position 104, with an F-ration of 6.1. A nearly suggestive association (F-ratio = 6.3) was identified on SSC 5 for AVBF in a similar region detected for LLUM.

Discussion

The biology of fat accumulation is multifaceted, and the relationships among the components are extremely complex. Adipose tissue is where the body stores excess metabolizable energy. However, metabolizable energy intake and its partitioning are affected by many factors, such as appetite, feed composition, maintenance requirements, and lean growth potential. Genes, or identified QTL, that affect fat accretion could have an impact on one or more facets of fat biology. We may gain some insight into the physiological or biological process that the QTL affects by determining what other traits are affected. Unfortunately, an understanding of the process is needed before logical positional candidates can be selected.

A considerable number of loci have been identified that affect fat accretion in humans and mice. However, few seem to be within regions homologous to those detected in this study. One QTL mapped in humans near the tumor necrosis factor alpha gene (**TNFA**) in a Pima Indian population (Norman et al., 1995) could be homologous to the QTL mapped to SSC 7 in this study. The TNFA is located within the major histocompatibility region, which is located on HSA 6p21.3 in humans (Nedwin et al., 1985) and on SSC 7p1.1–q1.1 in pigs (Solinas et al., 1992). The TNFA maps to relative position 58 cM on SSC 7 along with TNFB (Rohrer et al., 1996), well within the confidence interval for the QTL peak detected on SSC 7. Norman et al. (1995) selected the TNFA because its expression is elevated in various obese mouse and rat lines (Hotamisligil and Spiegelman, 1993). Unfortunately, no sequence polymorphisms within the coding or promoter regions that segregated with the observed phenotype were detected (Norman et al., 1995). Taylor and Phillips (1997) detected an obesity locus on MMU 17 near the centromere in mice. The region detected is not near the major histocompatibility complex, but there are a few genes in that region that also map to HSA 6p21. In our results, the maximum F-ratio for the six measures of fat was usually close to the location of TNFA, but we are unable to exclude a large portion of the adjacent chromosomal regions.

In mice, three putative QTL for body weight were detected residing on the X chromosome (Dragani et al., 1995), but no measures of body composition were recorded. They named the loci Bw1, Bw2, and Bw3. York et al. (1997) found a QTL for body fat on the X chromosome in mice using a different cross, which likely corresponds to Bw3 identified by Dragani et al. (1995). Very few genes have been linked in the swine genome to SSC X, so it is difficult to draw conclusions from comparative mapping data. Hu et al. (1997) reported linkage information on three genes for SSC X and were unable to detect any rearrangements in gene order between pig and human. Based on this crude comparative map of pig, human, and mouse, the QTL identified in this study possibly lines up with Bw2; however, the mouse X chromosome has had numerous rearrangements and any of the Bw loci are possible.

The only genomic scan conducted for carcass composition was based on a wild boar × Large White F_2 population (Andersson et al., 1994). They detected a significant region on SSC 4 for fat deposition (near position 48 on our map). We were unable to confirm this QTL, but that is likely due to the different germplasm being compared. Rothschild et al. (1995) detected a QTL for backfat near the major histocompatibility complex in swine on SSC 7 in a Chinese × North American germplasm comparison. Even though we also detected a significant QTL near the same position (ours is ~10 cM closer to the centromere), this QTL presented transgressive variation in our study, but the QTL detected by Rothschild et al. (1995) did not. Again, the germplasm compared was not identical, but one would expect the contrast to be similar. The difference in the estimate of the effect could be due to sampling, or Meishan pigs may possess an allele that expresses considerably leaner tissue than the alleles present in the other Chinese breeds compared by Rothschild et al. (1995). Genotype × environment interactions may exist between the QTL and differences in management or nutrition between experiments, similar to what has been observed in QTL studies of tomato (Paterson et al., 1991).

Genetic and environmental correlations between all of the measures of backfat are assumed to be high and positive. Therefore, caution should be taken when evaluating putative QTL that were not significant. The argument supporting the region on SSC 14 is rather weak, if the genetic and environmental correlations are taken into consideration. If all four of the individual measurements taken for backfat were measures of the same trait (subcutaneous fat deposition) and controlled by the same genes, then the most appropriate and powerful analysis would be the one with average backfat as the dependent variable. The average of three independent measures of the same trait would have less error associated with the value resulting in a lower residual mean square. For the QTL detected on SSC 1 and 7, this seems to be the case. The F-ratio for AVBF was the largest and most significant. However, results for many of the other detected regions do not fit this pattern.

The difference between the two breed types (¾ Meishan-¼ White composite vs ¼ Meishan-¾ White composite) was over 5 mm for FRIB and LLUM, and it was less than 2 mm at LRIB representing 13.8, 18.6, and 9.8% of the mean values, respectively. The QTL detected on SSC X seems to have its greatest influence on fat deposition over the midsection of the pig. Among the regions that display suggestive evidence of QTL for backfat, two regions seemed to affect only FRIB, two regions for LLUM, and two regions for either LRIB or 10th. These results suggest that the different measures of backfat may be controlled by different, but not mutually exclusive, subsets of genes. Many genes, and probably those with the largest effects, have a general effect on fat deposition (SSC 1 and 7), and other genes may be more specific and affect fat deposition at particular regions of the body.

Most of the QTL detected seem to be additive (Table 2). The only region with a considerable dominance deviation was SSC 13 for 10th. Transgressive variation was detected for all traits affected by regions on SSC 7 and 10. The only significant region of these was SSC 7. Transgressive variation has been identified in many plant QTL studies. Most interesting was the findings of Tanksley and McCouch (1997), who reported that alleles present in an undeveloped type of tomato were more desirable than those present in a high-producing selected strain. They propose that these desirable alleles were lost in improved lines through genetic drift that occurred during bottlenecks in their development (Tanksley

and McCouch, 1997). Bottlenecks in the development of livestock species may be even more severe than in plants because exotic germplasms are usually introduced via the importation of a small number of select males.

The importance of these findings is manifold. First, the identified regions are locations that contain genes affecting fat deposition. It is plausible that allelic variation will also exist in commercial populations of swine for these genes. This hypothesis should be tested before these results are applied to commercial swine populations that do not contain Meishan germplasm. Further, by knowing where genes that affect fat deposition exist, we can identify the gene to further our knowledge on inheritance of quantitative traits and whole-animal biology. Next, these results can be used to produce composites between Meishan and western swine with improved performance. Through marker-assisted selection, alleles that confer increased fat deposition can be eliminated to produce a leaner composite population. If there are no antagonistic pleiotropic effects with reproduction or linked genes, a composite could be produced that possesses the reproduction rate of Meishan pigs but the carcass composition of the other contributing breed. Selection for segments from Meishan pigs for SSC 7 and 10 may be beneficial because of their transgressive effects for carcass leanness.

Additional markers should be typed for the identified regions to obtain more precise estimates of the location of the QTL and attempt to determine whether the observed effect is due to a single gene or to a cluster of closely linked genes. After the position has been refined, comparative mapping of the regions would supply positional candidate genes to be tested. Additional analyses should be conducted to determine whether epistatic interactions exist between the detected loci.

Implications

The findings from this study have advanced our understanding of the inheritance of quantitative characters. The detected regions should be tested in other, more commercially relevant populations of swine to determine whether allelic variation for these regions also exists. If so, then these findings present the information necessary to initiate marker-assisted selection for carcass composition. In addition, these results may advance our understanding of the genetics of fat deposition if the genes that cause the observed effects can be identified. Further studies are necessary to determine epistatic interactions of the identified regions with other loci.

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